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ORIGINAL ARTICLE

Laying date depends on territorial breeders' age, climatic conditions and previous breeding success: a long-term study (2004–2021) with Bonelli's eagle in Spain

Andrés López-Peinado[1] · **Pascual López-López**[1]

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Abstract

Adjustment of reproductive timing within the annual cycle is a crucial issue for both offspring and parents' survival, and breeding success. Early laying date is closely related to successful breeding outcome and better survival. Obtaining long datasets on threatened long-lived species' breeding performance can contribute to their conservation. Using field observations and telemetry information, here we analyse how laying date of an endangered long-lived raptor varies with nest characteristics, individual factors and climatic variables during an 18-year (2004–2021) study period in eastern Spain. To this end, we estimated how environmental and individual variables affect laying date. Our results showed that average laying date in our study area took place on February 17th. Laying date showed no trend during the study period. Nests placed in higher elevations showed delayed laying dates. Territories occupied by adults with previous successful experience and high brood size showed earlier laying dates. Current year laying date was highly correlated with previous year laying date. Colder territories delayed laying date and the minimum temperature of the previous December were negatively correlated to previous laying date. Our results highlight the importance of experienced birds able to adjust timing of reproduction to maximise biological fitness. High adult mortality allows sub-adults to settle as breeders and jeopardises species' persistence. Therefore, the reduction of mortality of territorial birds is of the outmost importance to improve the conservation status of declining long-lived species such as the Bonelli's eagle (*Aquila fasciata*).

Keywords *Aquila fasciata* · Breeding ecology · Raptors · Territory · Weather

Zusammenfassung

Das Legedatum hängt vom Alter der territorialen Brutvögel, von den klimatischen Bedingungen und vom vorherigem Bruterfolg ab: eine Langzeitstudie (2004–2021) am Habichtsadler in Spanien.

Die Anpassung der Fortpflanzungszeit im jährlichen Zyklus ist eine entscheidende Frage für das Überleben sowohl der Nachkommen als auch der Eltern sowie für den Bruterfolg. Ein frühzeitiges Legen ist eng mit einem erfolgreichen Bruterfolg und einer besseren Überlebensrate verbunden. Die Erfassung von Langzeitdaten zur Brutleistung gefährdeter, langlebiger Arten kann zu deren Erhaltung beitragen. Unter Verwendung von Feldbeobachtungen und Telemetriedaten analysieren wir hier, wie sich das Legedatum eines gefährdeten, langlebigen Greifvogels mit Nestcharakteristika, individuellen Faktoren und klimatischen Variablen während eines 18-jährigen Untersuchungszeitraums (2004–2021) in Ostspanien verändert hat. Zu diesem Zweck haben wir geschätzt, wie Umwelt- und individuelle Variablen das Legedatum beeinflussen. Unsere Ergebnisse zeigten, dass das durchschnittliche Legedatum in unserem Untersuchungsgebiet am 17. Februar stattfand. Das Legedatum

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✉ Andrés López-Peinado
Andres.Lopez-Peinado@uv.es

[1] Movement Ecology Laboratory, Cavanilles Institute of Biodiversity and Evolutionary Biology, University of Valencia, C/Catedrático José Beltrán 2, E-46980, Paterna, Valencia, Spain

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zeigte keinen Trend während des Studienzeitraums. Nester in höheren Lagen wiesen verzögerte Legedaten auf. Territorien, die von Erwachsenen mit früherem erfolgreichen Brutvogel-Erlebnis und hoher Brutgröße besetzt waren, zeigten frühere Legedaten. Das aktuelle Legedatum war stark mit dem Legedatum des Vorjahres korreliert. Kältere Territorien verzögerten das Legedatum, und die Mindesttemperatur des vorherigen Dezembers korrelierte negativ mit dem vorherigen Legedatum. Unsere Ergebnisse unterstreichen die Bedeutung erfahrener Vögel, die in der Lage sind, den Zeitpunkt der Fortpflanzung anzupassen, um die biologische Fitness zu maximieren. Hohe Sterblichkeit von Adulten ermöglicht es Subadulten, sich als Brutvögel niederzulassen und gefährdet die Beständigkeit der Art. Daher ist die Reduzierung der Sterblichkeit territorialer Vögel von höchster Bedeutung, um den Erhalt des Rückgangs langlebiger Arten wie dem Habichtsadler (*Aquila fasciata*) zu verbessern.

Introduction

The adjustment of reproductive timing within the annual cycle is a crucial issue for both offspring and parents' survival (Perrins 1970; Bauwens and Verheyen 1985; Eitam et al. 2005; Dawson 2008; Wong and Forrest 2021). Seasonality constrains reproductive timing across species (Perrins 1970; Verhulst et al. 1997; Houston and McNamara 1999; Thomas et al. 2001; Davies and Deviche 2014) through intra-annual food availability and climatic variations, especially for those which do not thermos regulate on their first days of life or are exposed to inclement weather conditions without possibility to shelter (e.g. nidicolous birds) (Beecham and Kochert 1975). Climatic conditions influence reproductive timing and productivity (Cavé 1968; Adamcik et al. 1979; Village 1986; Gargett 1977; Kostrzewa 1989; Amato et al. 2021), particularly because climate severity (both the extreme cold at the beginning of the breeding season and the excessive heat towards the end of the breeding season) can reduce brood viability (Tjernberg 1983; Marti and Wagner 1985; Swenson et al. 1986; Kostrzewa and Kostrzewa 1990, 1991; Huchler et al. 2020). In general terms, despite evidence given about costs of early breeding (Nilsson 1994; Brown and Brown 2000), early reproducing individuals can be more successful than late breeders (Perrins 1970; Perrins and McCleery 1989; Hochachka 1990; Svensson 1997; Verboven and Visser 1998; Bêty et al. 2004; Verhulst and Nilsson 2008; Berger-Geiger et al. 2019). Higher survival of the breeders mediated by an earlier independence of fledglings or high food availability for parents to allow recovery after breeding could facilitate advancing laying date as well (Verhulst and Nilsson 2008). In addition, earlier nestlings are usually in better body condition (Cornell et al. 2021), are less affected by parasites and show higher fledging rates (Richner et al. 1993; Dudek 2017) than late nestlings, so benefits of early reproduction affect both parents and offspring.

In the light of these evidences, it seems necessary for birds to adjust their reproductive timing and phenology to seasonality. Some studies have emphasised the role of extrinsic factors (i.e. breeding territory quality) as the main driver of this phenological adjustment (Olsen and Marples 1993; Coppes et al. 2021), whereas other studies have focussed on intrinsic factors (i.e. individual quality) as the main causes underlying reproductive timing improvement (Korpimäki et al. 1995; Verhulst and Nilsson 2008; Lamarre et al. 2017). Although laying date is a well-studied topic, little is known about long-lived raptors' laying date adjustment. Due to raptors' ecology and their usually limited population size, obtaining large data sets, it is often difficult, and the main studies in this field have been focussed on small raptors, mostly of species breeding in nest boxes (Dijkstra et al. 1990; Risch and Brinkhof 2002; Carrillo and González-Dávila 2010; Catry et al. 2012; Bragin et al. 2017; Rosenfield et al. 2017; Huchler et al 2020) or have focussed their attention to migratory raptors and laying date adjustment (Sergio 2003). Nonetheless, long-term studies focussed on laying date of long-lived raptor species are still scarce (Smith and Murphy 1979; Steenhof et al. 1997; Gil-Sánchez 2000; López-López et al. 2007; Margalida et al. 2014).

Our main aim is to analyse how laying date varies in a long-lived raptor. We are interested in analyse (1) how Bonelli's eagle's laying date has changed over the years in the present context of climate change; and how laying date varies with (2) nest characteristics (i.e. altitude, orientation, nest type), (3) territorial breeders (i.e. parents' age, previous success, change of nest with respect to the previous year), and (4) climatic variables (i.e. minimum and average temperature) amongst seasons. To this end, we monitored the laying date of the Bonelli's eagle, a long-lived endangered raptor, during an 18-year period in eastern Spain in order to test its variation with climate, altitude, parents' age and previous experience.

According to our first goal (1), we hypothesise that Bonelli's eagle population would show a trend to earlier laying dates as consequence of climate change (H1); for the second goal (2), we hypothesise that that more covered nest, situated in lower altitudes and south-oriented would show earlier laying date (H2); our third hypothesis (3) is that adults breeding in territories with earlier previous laying date, previous success, higher previous year brood size and without nest changes would have earlier laying dates (H3); for the last objective (4), we hypothesise that lower and more extreme temperatures (lower average and minimum temperatures during previous autumn) before laying period would delay laying date (H4).

The results of this work could be of interest to researchers, ornithologists and eventually, practitioners. Long-term studies are essential in ecology to improve our understanding of process-driving factors and to improve management policies (Hughes et al. 2017). Hence, a detailed knowledge of how laying date varies over time would allow environmental authorities to determine the most sensitive periods for this species and thus to improve conservation actions.

Materials and methods

Study area

Our study area encompasses the Castellón province (6670 km^2, east of Spain). This is a Mediterranean region that includes elevations from sea level at the coastal line to 1814 m.a.s.l. at the highest mountain, with some abrupt changes in some areas. The study area's ruggedness is ought to the confluence of two mountain ranges: the Iberian System (northwest–southeast-orientated) and the Catalánides (east–southeast-orientated). Mean annual temperature varies from 17 °C at lower and coastal areas to 8 °C at the highlands. Annual mean precipitation varies from 400 to 900 mm, with the highest values recorded on autumn and the driest during summer. The landscape is composed by Mediterranean forests and shrublands where prevalent species are pines (*Pinus* spp.) and oaks (*Quercus* spp.). The study area is intermingled with non-irrigated and irrigated cultivation zones. This landscape maintains abundant prey populations for raptors, including mainly partridges, pigeons, rabbits, hares and lizards, part of the Bonelli's eagle's diet (Ontiveros 2016).

Study species

The Bonelli's eagle (*Aquila fasciata*) is a long-lived raptor distributed from the European Mediterranean region to South-east Asia (Cramp and Simmons 1980). Although this is a well-studied species, the only study about laying date was conducted by Gil-Sánchez (2000) in which he described the relationship between altitude and laying date in south-eastern Spain. Notwithstanding, other habitat factors that might be affecting the laying date have not been studied in detail.

The Bonelli's eagle usually breeds on cliffs, sometimes on trees (Arroyo et al. 1995) and, in extremely rare cases, on electric pylons (Hernández 1999). In Mediterranean Spain, the breeding season starts in October–November, with breeders delivering branches to the nest and starting courtship. By November–December, courtship flights intensify, and mating takes place usually from December to April (Real 1982). Laying date varies with latitude, starting in January until the first weeks of April. Replacement clutches after early breeding failure are usually rare (Moleón et al. 2009). In our study area, the mean laying date was 18 February ± 16 days, ranging from 27 January to 28 March (López-López et al. 2007). Incubation period usually spans 37–41 days (Arroyo et al. 1995).

Fieldwork

Between 2004 and 2021, we monitored once a month (from January to June) all territories occupied by Bonelli's eagles, as well as areas that historically had been occupied but remained vacant even though the habitat appeared to be suitable for the species (López-López et al. 2006). Observations were made with a 20–60 × Leica Televid 77 and Swarovski telescopes during clear days at > 300 m from nesting cliffs to avoid disturbance to eagles (López-López et al. 2004, 2006, 2007). Every year we recorded nest type, orientation, change with respect to the nest occupied the previous year, breeders' ages (adult, subadult or mixed breeding pair), number of nestlings and number of fledglings (Table S1). Parents' age was determined according to plumage characteristics (i.e. birds on their third to fourth calendar year were considered as sub-adults and birds over their fifth calendar year were considered as adults). A chick was considered to have fledged when it reached 80% of the fledging age (i.e. more than 60 days old) in the last visit, provided that at this age nestlings are fully feathered and ready to fly (Carrete et al. 2002; Gil-Sánchez et al. 2004; López-López et al. 2022).

Laying date was estimated from nestlings' age following López-López et al. (2007), by their feather development through accurate observations with field telescopes according to the figures given by Torres et al. (1981) and Gil-Sánchez (2000). This method has an error of ± 3 days and gives the laying date by adding 39 days to the estimated nestling's age of the older chick (the mean incubation period for the species) (Arroyo et al. 1995). All observations of nestlings' age were done by the same person (the senior author of this paper) during the overall study period to avoid biases due to different observers. Moreover, since 2015, we started a research project in which 53 territorial breeders were captured and tagged with GPS/GSM/ACC dataloggers (Perona et al. 2019; Morollón et al. 2022a, b). Thereby, laying date, incubation length and consequently nestlings' age were accurately determined and calibrated by the combination of telemetry, accelerometry information and field observations (López-López et al. 2022; López-López 2022).

Climatological data

For this study, we generated a climatological database with monthly mean, maximum and minimum temperature, rainfall and days with frosts for the 2007–2021 period, the longest time series for which data were available. We collected climatological data from 200 stations distributed throughout the Castellón province from the AVAMET website (https://www.avamet.org/). With this information, we generated interpolated rasters using the Inverse Distance Weighted method (IDW) corrected by a digital terrain model (MDT50) for temperature ones using the "sf" (Pebesma 2018), "sp" (Pebesma and Bivand 2005), "raster" (Hijmans 2021) and "gstats" (Pebesma 2004) R packages (R Core Team 2021). We extracted the climatological data of each year nests' coordinates from the interpolated climatological rasters.

Data analysis

All analyses were performed using R version 4.1.0 (R Core Team 2021). To estimate how nest characteristics, territorial breeders and climatic variables affect laying date, we built General Linear Mixed Models (GLMMs). GLMMs were fitted using the R package lme4 (Bates et al. 2013), with a Gaussian error distribution and the identity link. We considered explanatory variables related to nest characteristics (altitude, nest type, and orientation divided into two axis: northing and easting), territorial breeders characteristics (laying previous, sub-adults as breeders, nest change, preceding success), climate of winter/laying period (January to March) and autumn/pre-laying period (October to December) for the current and the previous year. "Territory" was included in GLMMs as a random term to control for spatial pseudo-replication. To model laying date variation according to nest characteristics and territorial breeders features, we built GLMMs for each individual variable (i.e. making as many single two variable regressions as explanatory factors) and ensure that all the models were more informative than the random or null model (Omnibus test). For choosing which season and month were more relevant for predicting laying date variation according to climatic variables, we built GLMMs for each single variable. To this end, we used the function "model.sel" from the package MuMIn version 1.47.5 (Bartoń 2009) that selected between all the GLMMs and the null model. An information–theoretical approach based on Akaike's Information Criterion (AIC) was then used for model selection (Burnham and Anderson 2002), selecting models with a $\Delta AIC \leq 2$ units as the best models. Models accuracy has been checked through examination of residuals.

Results

Laying date trend and climate change

Overall, after 18 years of Bonelli's eagle breeding monitoring in 35 territories, we recorded 431 breeding attempts with 434 fledglings. Of these, we obtained 200 accurate laying dates of which 37 cases were determined by the combination of telemetry information and field observations. On average, 24 ± 4 nests were occupied per year (range = 17–30), 24 ± 6 fledglings fledged each year (range = 15–36), and 11 ± 3 accurate laying dates were recorded per year (range = 2–15).

Bonelli's eagle laid, on average, on February 17th (48th Julian day of the year) in our study area. The earliest records of laying date were January 24th (2012) and 26th (2005, 2014 and 2020). The most delayed date was recorded on April 2nd (2010). Laying date did not show any trend over time (Fig. 1). Although a slight increase in mean temperature was observed in all territories, there was no homogeneous response of laying date across different territories (Fig. S1).

How laying date changes with nest characteristics

We found that coverage of the nest does not show a clear relationship with laying date. Compared to the most exposed nest type (tree nest), open shelf nests (estimate = 3.628; $p = 0.141$), covered shelf nests (estimate = −0.522; $p = 0.838$) and cave nests (estimate = 4.720; $p = 0.140$) present a non-significant higher average laying date, slightly lower for the covered shelf nests (Figs. 2A, S3). We did not find significant differences between West and East nest orientation (estimate = 1.001; $p = 0.522$), but south-oriented nests were almost significantly later for laying dates than north-oriented (estimate = 2.898; $p = 0.051$) (Figs. 2B and C, S4, S5). South-oriented nests were less frequent in low altitudes (Fig. S2). We also found that an increase in altitude was clearly related with a delay in laying date (estimate = 0.019; $p = 0.032$) (Figs. 2D, S6).

How laying date variates with territorial breeders' characteristics

Territories occupied by at least one subadult laid eggs later (estimate = 4.707; $p = 0.003$) (Figs. 3A, S7). We did not

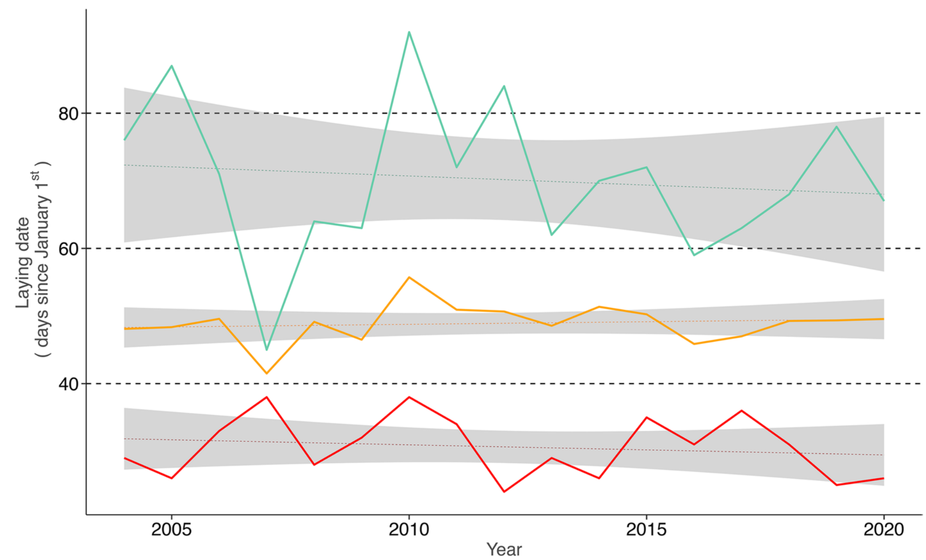

Fig. 1 Annual variation in Bonelli's eagle laying date over an 18-year study period (2004–2021) in eastern Spain. Maximum (blue line), minimum (red line) and average (yellow line) laying date values are shown. Linear trends (dashed lines) with standard error (grey smooth) are also shown (color figure online)

find significant relationships between nest change and laying date (estimate = −0.538; $p = 0.548$) (Figs. 3B, S8). Territories in which reproduction was successful in the previous year laid eggs earlier (estimate = −2.574; $p = 0.008$) (Figs. 3C, S9). Indeed, pairs that raised two chicks the previous year laid eggs earlier than pairs with zero chicks (estimate = −3.662; $p = 0.001$) (Figs. 3D, S10). Previous year laying date was highly correlated with current year laying date (estimate = 0.505; $p < 0.001$) (Figs. 4E, S11).

How laying date variates with climatic variables

We found that the best model predicting laying date variation according to climatic variables includes the minimum temperature of the previous autumn (Table S2). Pairs breeding in territories with more extreme minimum temperature during the previous autumn showed later laying dates (estimate = −0.753; $p = 0.036$) (Figs. 4, S12). Autumn was composed by the months of October, November and December, but we found that the minimum temperature of December was the one that predicted better the laying date (Table S3) and showed a stronger relation (estimate = −0.679; $p = 0.041$) (Figs. 5, S13).

Discussion

Long-term studies are essential to achieve a better understanding of the mechanisms underlying how life history parameters change over time. Yet, ecological constraints act as selective pressures determining key events of the annual cycle in long-lived animals. Several studies have found that some birds advance their laying date in response to environmental conditions (e.g. Visser et al. 1998; Both et al. 2004; Shipley et al. 2020). In contrast, our results support the idea that long-lived predators could take more time to adapt their breeding phenology in relation to environmental change. Other factors, such as breeders' experience and/or territory quality, could be also important in determining timing of reproduction. Our results showed that age of breeders and previous territorial positive breeding performance are adequate predictors of laying date. Climatic conditions could influence fitness of some raptor species. However, raptors are able to mitigate harsh weather environments by selecting the most efficient places for nesting. This is the first study in which Bonelli's eagle laying date has been studied according to different climatic, territorial breeders and nest variables.

Laying date trend and climate change

Overall, after this 18-year study and in contradiction to our first hypothesis, we did not observe any significant trend of laying date over time. In contrast to other bird species that experienced presumed effects of climate change on their timing of reproduction (Both et al. 2004; Knudsen et al. 2011; Brommeret al. 2012), Bonelli's eagle's laying date remained steady throughout the study period.

On the one hand, climate change is likely to impact all trophic levels (Chambers et al. 2005). Nonetheless, most raptors, as long-lived top predators, would be less responsive to rapid environmental changes and might be able to buffer the effects of climate change, which would be evident in the

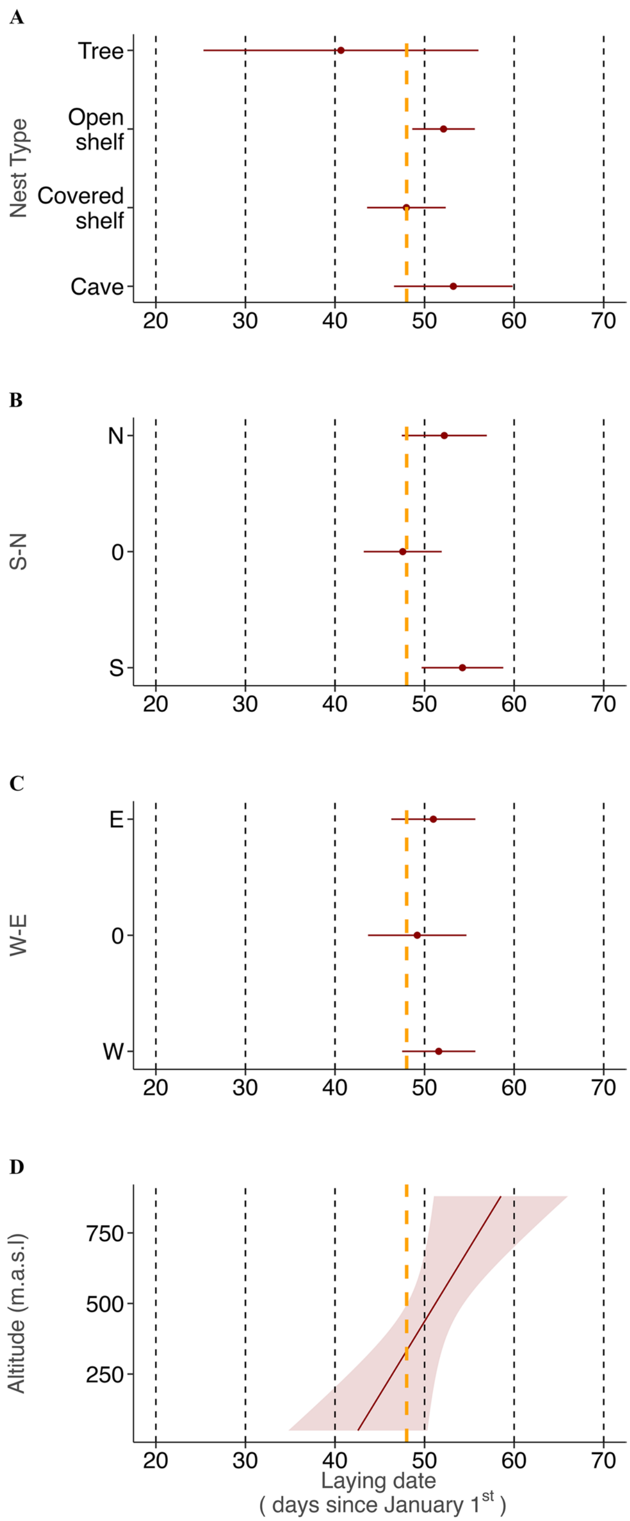

Fig. 2 Predicted laying date according to the different nest type categories (**A**), nest orientation in the N–S axis (**B**) and E–W axis (**C**) and nest altitude (**D**). Red dots show the average value for each category and the bars show the 95% CI. Red solid line shows the predicted linear relationship between altitude and laying date and the red shadow shows the 95% CI. Yellow dashed line indicates the average laying date in the area (48th calendar day) (color figure online)

long term (Both et al. 2009). The bigger body size could mitigate these effects (Brommer 2008), or they might not be observed on top predators if they do not depend on seasonal food peaks and could mitigate climate change effects on prey availability by switching preys according to its availability (Rand and Tscharntke 2007). Furthermore, complex ecological networks could show compensatory mechanisms that might buffer these effects (Brown et al. 2001).

How laying date variates with nest characteristics

In agreement with Gil-Sánchez (2000) and our previous results reported in López-López et al. (2007), we found a significant delay in laying date as elevation increases. The relationship detected here is not so strong as in Gil-Sánchez (2000), but this difference could be explained because Gil-Sánchez's study area accounts for a wider altitude range (0–3492 m.a.s.l) than ours (0–1814 m.a.s.l).

Remarkably, early laying date appears in coastal territories, with higher average temperatures, less temperature range, milder minimum temperatures and less days of frosts. In agreement with Olsen and Marples (1993), environments that are more continental delay laying date. This could be explained by the unpredictable weather changes that could have a negative effect in breeding performance by reducing the viability of younger nestlings (Cavé 1968; Beecham and Kochert 1975; Marti and Wagner 1985; Village 1986; Swenson et al. 1986; Kostrzewa and Kostrzewa 1990).

Therefore, we expected that nests placed on covered shelves showed earlier laying dates than those placed on open shelves. The protection given by the cover against inclement or extreme weather conditions could allow advancing reproductive phenology avoiding negative weather impacts, particularly early breeders that start reproduction during late winter months (Cavé 1968; Beecham and Kochert 1975; Marti and Wagner 1985; Village 1986; Swenson et al. 1986; Kostrzewa and Kostrzewa 1990). Nonetheless, the relationship that we found was not strong enough to support this hypothesis.

For the same reason, we expected to find earlier laying dates in south-oriented nests, but we did not. We found less south-oriented nests in the lower areas and that can be the reason of the disagreement with the hypothesis (H2). Our study area is characterised by an abrupt orography and Mediterranean climatic conditions where eagles can select where to build their nest from a wide variety of rocky cliffs (López-López et al. 2004, 2006) and maybe the selection of orientation as a microclimate solution to avoid extreme warm weather in the low areas and extreme cold weather on high areas mitigate the expected relationship, but we have not tested specifically the availability of possible nest building places in the area.

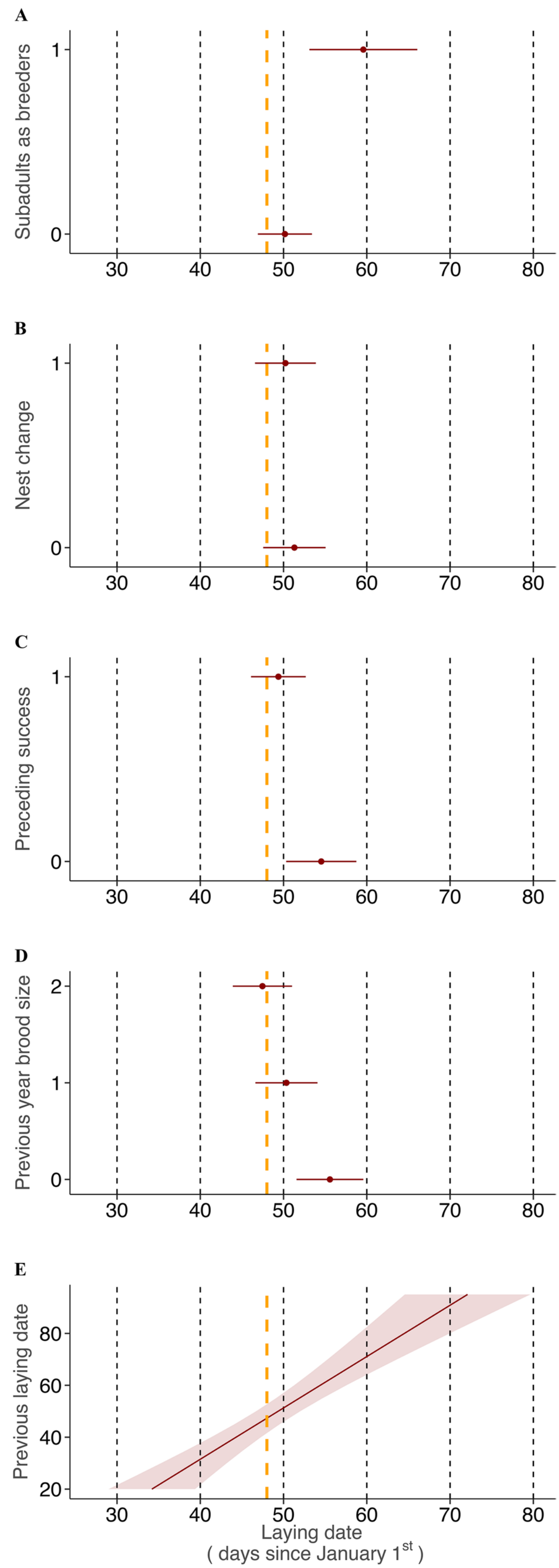

Fig. 3 Predicted laying date according to the presence (1) or absence (0) of at least one subadult as breeder (**A**), nest change (1) or not (0) regarding the previous year (**B**), previous year breeding success (1) or failure (0) (**C**), number of chicks fledged the previous year on the same territory (**D**) and previous year laying date (**E**). Red dots show the average value for each category and the bars show the 95% CI. Red solid line shows the predicted linear relationship between previous and current year laying date and the red shadow shows the 95% CI. Yellow dashed line indicates the average laying date in the area (48th calendar day) (color figure online)

How laying date variates with territorial breeders' characteristics

Adult breeders occupying territories in which previous year breeding was successful laid eggs earlier than other individuals. Our results are in agreement with previous studies in birds (e.g. Perdeck and Cavé 1992; Moreno 1998; Risch and Brinkhof 2002; van de Pol and Verhulst 2006; Verhulst, and Nilsson 2008). In addition, we found that pairs composed by at least one subadult as breeder had a later laying date. This suggests that experience and age counts, especially in long-lived territorial birds. Older birds know better their territories and optimise hunting efficiency. More life-experience allows better fitting of breeding timing and enhances food acquisition to feed brood and to maintain parental body condition (Verhulst and Nilsson 2008).

Importantly, population dynamics and reproduction of long-lived predators are highly influenced by adult and subadult mortality. High adult mortality allows sub-adults to settle as breeders and jeopardises species' persistence, as observed in our study area (authors, unpublished data). Previous studies agreed that increasing proportion of subadults as breeders in long-lived raptors is an early warning signal of population decline (Ferrer et al. 2003; Gil-Sánchez et al. 2005; Carrete et al. 2006). We show that the presence of subadult birds as breeders is negatively related with the breeding time adjustment, as delayed laying date is related with lower productivity (López-Peinado and López-López 2023). Therefore, it is important to reduce adult mortality and preserve experienced breeders of long-lived raptors.

Nest changes could be more frequent at low areas because the human presence and disturbance is more noticeable there (Whitfield et al. 2004; Perona et al. 2019). Furthermore, nest change was more frequently observed in pairs that had switched one of its members during the previous year, and hence we expected a delay in laying date as consequence of the replacement of one of the territorial breeders or could be related to new pairs' courtship display (which, as in other "building-nest" birds, includes nest choice and building) (Soler et al. 1998). Nonetheless, we did not find enough evidence of this delay in laying date.

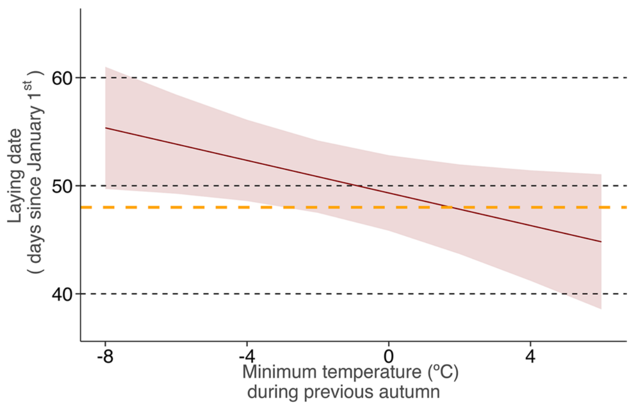

Fig. 4 Predicted laying date according to minimum temperature registered at the territory during the previous autumn (red solid line, red shade shows 95% CI). Yellow dashed line indicates the average laying date in the area (48th calendar day) (color figure online)

How laying date variates with climatic variables

Bonelli's eagles are closely linked to warm temperatures and they find their optimal habitat in these areas (Muñoz et al. 2005; Ontiveros and Pleguezuelos 2003), so it was expected to find that lower temperatures during the pre-laying period would delay laying date. We found a clear relationship between the minimum temperature registered in the territory during the previous autumn (and more specifically during December) and laying date. The costs of early breeding are well described (Nilsson 1994; Brown and Brown 2000). Even though early breeders usually show better breeding performance (Perrins 1970; Perrins and McCleery 1989; Hochachka 1990; Svensson 1997; Verboven and Visser 1998; Bêty et al. 2004; Verhulst and Nilsson 2008; Berger-Geiger et al. 2019), eagles delay laying date as consequence of colder autumns in order to avoid cold temperatures that could make the eggs fail or the nestlings die. In fact, Bonelli's eagle breeding performance in our study area was lower in colder areas with higher rate of winter frosts (López-Peinado and López-López 2023).

Our 18-year study contributes to the understanding of the intricate mechanisms underlying Bonelli's eagle breeding phenology and highlights the importance of long-term studies in comprehending the responses of long-lived animals to environmental changes. The resilience of these top predators to climate change, as well as the influence of ecological constraints and breeding experience on their reproductive timing, provides valuable insights for the conservation and management of this iconic species. Further research is warranted to explore the specific mechanisms driving laying date trends and to develop effective conservation strategies to safeguard the future of Bonelli's eagles and other raptors in the face of changing environmental conditions. Moreover, the relationship we showed between age and experience of the breeders and the breeding outcome has appeared in other species before and we encourage the idea of using presence of subadult birds as breeders may serve as an early warning signal of population decline in this species and we emphasise the relevance of preserving experienced breeders to maintain population dynamics and reproduction in long-lived predators.

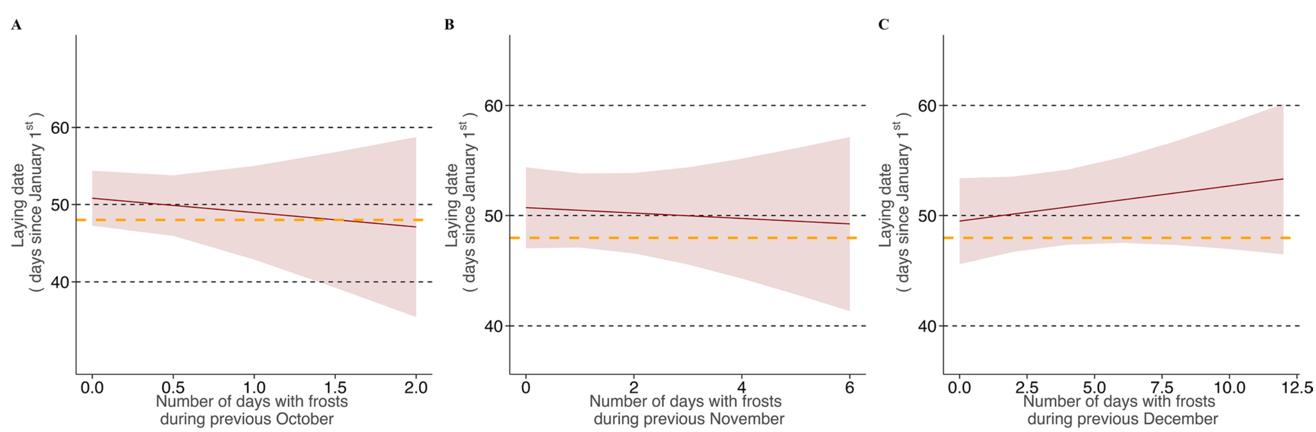

Fig. 5 Predicted laying date according to minimum temperature registered during the previous autumn months: October (**A**), November (**B**), December (**C**). Red solid line shows the predicted linear relationship between the monthly minimum temperature registered on the territory and the laying date and the red shadow shows the 95% CI. Yellow dashed line indicates the average laying date in the area (48th calendar day) (color figure online)

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Data availability Data used in this study are publicly available in the online data repository Movebank (www.movebank.org), project 'Bonelli's Eagle University of Alicante Spain' (project ID = 58923588), and project 'Bonelli's Eagle University of Valencia Spain' (project ID = 193515984).

Declarations

Conflict of interest The authors have no conflict of interest to declare.

Ethics approval This is an observational study, so no permission was necessary for field monitoring. Trapping and marking of eagles with GPS transmitters during 2015–2021 was done under permissions issued by the Wildlife Service of the Valencian Community Regional Government (Generalitat Valenciana, Spain).

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